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Research Article

Outline, phylogenetic and divergence times analyses of the genus *Haploporus* (Polyporales, Basidiomycota): two new species are proposed

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Abstract

Haploporus species have a worldwide distribution and 27 species have been accepted. In this study, two new species, *Haploporus crystallinus* and *H. dextrinoideus*, are proposed from South America, based on the molecular fragments (ITS, LSU and mtSSU) and morphological evidence. Molecular clock analysis was performed and the result suggests that the ancestor of Polyporales originated between the Late Jurassic and Early Cretaceous period, with a mean stem of 159.8 Mya [95% higher posterior density (HPD) of 142.4–184.1 Mya] and the genus *Haploporus* occurred at a mean stem of 108.3 Mya (95% HPD of 88.5–128.2 Mya). In addition, most species of the genus are diversified between 60.5 Mya and 1.8 Mya, during the Paleogene to Neogene. A key to the accepted species of the genus *Haploporus* is provided.

Key words: fungal diversity, new taxa, molecular clock dating, wood-inhabiting fungi

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Introduction

Currently, more than 155,755 species of fungi have been described worldwide, based on molecular analyses and morphological features and the numbers of fungal species have been rapidly increasing in the last two decades (https://www.speciesfungorum.org/Names/Names.asp, accessed 21 June 2023). For example, Kirk et al. (2008) recorded 487 species of the family Hymenochaetaceae in the 10th version of Dictionary of the Fungi, but 672 poroid species in 34 genera were recognised in 2022 (Wu et al. 2022a). Still, the fungal diversity is poorly known as only 4.10–7.08% fungal species have been described of an estimated 2,200,000–3,800,000 (Hawksworth and Lücking 2017; Wang et al. 2019).

The genus *Haploporus* Bondartsev & Singer, proposed by A. S. Bondartsev and R. Singer and typified by *Haploporus odorus* (Sommerf.) Bondartsev & Singer (Singer 1944), belongs to Polyporaceae, Polyporales, Agaricomycetes in Basidiomycota. The genus is characterised by: 1) basidiomata annual to perennial and resupinate to pileate; 2) hyphal system monomitic, dimitic to trimitic with clamped generative hyphae; 3) cyanophilous skeletal hyphae; 4) cyanophilous

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and ornamented basidiospores; and 5) causing a white rot (Singer 1944; Dai et al. 2002; Piątek 2003, 2005; Li et al. 2007; Shen et al. 2016; Zhou et al. 2019, 2021; Decock et al. 2021; Man et al. 2023).

A phylogenetic study suggested that the genus *Haploporus* was sister to the genus *Perenniporia*, based on the ITS + LSU + mtSSU + rpb2 + TEF1 sequences and 13 species have been accepted (Shen et al. 2016). Later, ITS + LSU and ITS + LSU + mtSSU sequences were used to reconstruct the phylogenetic relationships of the genus *Haploporus*, respectively (Zhou et al. 2019, 2021; Decock et al. 2021; Man et al. 2023), the results showing that they were compatible.

Until now, 27 species are accepted in the genus *Haploporus*, widely distributed in Africa, Asia, Europe, North America, Oceania and South America (Wu et al. 2022b; Man et al. 2023). In Africa, four species, *H. eichelbaumii*, *H. grandisporus*, *H. nanosporus* and *H. papyraceus*, are described (Decock et al. 2021). In Asia, 16 species are reported, accounting for 59.3% (16/27) of total species of the genus and are mainly found in China and Sri Lanka (Dai et al. 2004, 2007, 2021; Li et al. 2007; Dai 2012a, b; Shen et al. 2016; Zhou et al. 2019, 2021; Man et al. 2023). In Europe, three species are accepted, viz. *H. odorus*, *H. subtrameteus* and *H. tuberculosus* (Ryvarden and Gilbertson 1993; Zhou et al. 2019). In North America, four species are reported, including *H. alabamae*, *H. gilbertsonii*, *H. odorus* and *H. papyraceus* (Zhou et al. 2019). In Oceania, only one species, *H. pirongia*, is found from Australia and New Zealand (Zhou et al. 2019). In South America, four species are recorded from Brazil and Ecuador (Lira et al. 2018; Zhou et al. 2021; Man et al. 2023). Most species of the genus *Haploporus* grow on angiosperms, including branches, twigs, fallen trunks, stump, even living trees, while *H. latisporus* is the sole species growing on gymnosperm wood (Li et al. 2007; Zhou et al. 2019, 2021).

Molecular clock analyses provided new insights into the origin and evolution of fungi, such as reconstructing the divergence time of Basidiomycota and early-diverging fungi, based on multiple gene loci (Cao et al. 2012; Wu et al. 2014; Chen et al. 2015; Cui et al. 2018; He et al. 2019; Varga et al. 2019; Zhao et al. 2022a). The previous study suggested that divergence times of the order Polyporales, the genus *Polyporus* and its allied genera, originated about 141.81 Mya and 49–63 Mya years ago, based on six DNA fragments (Ji et al. 2022). The divergence times of *Haploporus* species have not yet been studied.

During the trips in South America, we collected some specimens of the genus *Haploporus* and carried out detailed studies combining morphology, phylogeny and molecular clock dating. Thus, two new species, *Haploporus crystallinus* and *H. dextrinoideus*, are described in this study.

Materials and methods

Morphological studies

In the present study, the newly-studied specimens of the genus *Haploporus* were collected from South America, deposited in the herbarium of the Institute of Microbiology, Beijing Forestry University (**BJFC**, China), the National Museum Prague of Czech Republic (**PRM**, Czech Republic) and the private herbarium of Josef Vlasák (**JV**, Czech Republic). The methods of morphological description

followed the previous study (Dai 2010; Chen et al. 2016). L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, n = x/y = number of spores (x) measured from a given number (y) of specimens (Yuan et al. 2017). The colour terms used by Anonymous and Petersen are followed (Anonymous 1969; Petersen 1996).

DNA extraction, PCR amplification and sequencing

Total genomic DNAs were extracted from dried specimens using a kit (Aidlab Biotechnologies, Beijing, China), following the manufacturer's instructions. Polymerase chain reaction (PCR) was used to amplify the partial fragments of the internal transcribed spacer (ITS), large subunit ribosomal RNA (LSU) and small subunit mitochondrial rRNA gene (mtSSU) with the fungal-specific primers, according to the previous studies (Zhou et al. 2019, 2021; Man et al. 2023). The amplification of the ITS, LSU and mtSSU partial fragments were carried out under the following conditions: for ITS and mtSSU partial fragments, an initial denaturation at 95 °C for 3 min, followed by 34 cycles at 94 °C for 40 s, 54 °C for 45 s and 72 °C for 1 min and a final extension of 72 °C for 10 min; for LSU partial fragments, an initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 50 °C for 1 min and 72 °C for 1.5 min and a final extension of 72 °C for 10 min (Zhou et al. 2019, 2021; Man et al. 2023). Sequencing was performed by BGI Tech Solutions (Beijing Liuhe Co., Ltd., Beijing, China) using the ABI-3730-XL DNA Analyzer (Applied Biosystems, Foster City, CA, USA). All the newly-generated sequences are deposited in GenBank database with the accession numbers listed in Table 1.

Phylogenetic analyses

The ITS, LSU and mtSSU partial sequences were aligned using MAFFT v.7 (Katoh and Standley 2013) and concatenated after excluding the poorly-aligned sites as dataset 1. The aligned dataset 1 was analysed using Maximum Likelihood (ML), Maximum Parsimony (MP) and Bayesian Inference (BI) phylogenetic analyses with RAxML v.8 (Stamatakis 2014), PAUP v.4.0b10 (Swofford 2002) and MrBayes v.3.2.7a (Ronquist et al. 2012), respectively, followed the previous studies (Zhao et al. 2021; Man et al. 2023). Additionally, the phylogenetic analyses of the aligned ITS, LSU and mtSSU partial sequences were also undertaken using RAxML v.8 (Suppl. materials 1: figs 1–3; Stamatakis 2014), respectively. The optimum model of the aligned dataset 1 was tested using the ModelTest-NG v.0.1.7 (Darriba et al. 2020). For ML and MP analyses, 1,000 bootstrap replications were carried out. For BI analysis, two million generations were conducted with random initial trees and the first 25% were set as burn-in.

Divergence time analysis

Dataset 2, consisting of 58 ITS and LSU partial sequences, was used to infer the divergence times of the species in the genus *Haploporus* (Table 1, Suppl. material 1: table S1 and file S1). The divergence time was estimated with BEAST v.2.6.5 (Bouckaert et al. 2014), following previous studies (Liu et al. 2022;

Table 1. Taxa information and GenBank accession numbers used in this study.

Species	Sample no.	GenBank Accession no.			Country	References
		ITS	LSU	mt-SSU		
Haploporus alabamae	Dollinger 895	KY264038	MK433606	MW463004	USA	Zhou et al. (2019)
H. alabamae	JV 1704/75	MK429754	MK433607	MW463005	Costa Rica	Zhou et al. (2019)
H. angustisporus	Dai 10951	KX900634	KX900681	MW463006	China	Zhou et al. (2019)
H. bicolor	Dai 19951	MW465684	MW462995	–	China	Zhou et al. (2021)
H. crassus	Dai 13580	MW465669	KU941865	–	China	Zhou et al. (2019)
H. crystallinus	**JV 2208/36**	**OQ919235**	**OQ919238**	**OQ919241**	**French Guiana**	**This study**
	FG-14-870	MT782653	MT777443	–	**French Guiana**	Decock et al. (2021)
H. cylindrosporus	Dai 15664	KU941854	KU941878	KU941903	China	Shen et al. (2016)
H. dextrinoideus	**JV 2211/1-J**	**OQ919237**	**OQ919240**	**OQ919242**	**Ecuador**	**This study**
	JV 2106/45-J	**OQ919236**	**OQ919239**	–	**Ecuador**	**This study**
H. ecuadorensis	JV1906/C10-J	MW465661	OP948227	OP948226	Ecuador	Man et al. (2023)
H. eichelbaumii	Congo 1	MT758256	MT758256	–	Congo	Decock et al. (2021)
	KE-17-238	MT758261	MT758261	–	Kenya	Decock et al. (2021)
H. gilbertsonii	JV 1611/5-J	MK429756	MK433609	MW463007	USA	Zhou et al. (2019)
H. grandisporus	KE-16-130	MT758242	MT758242	–	Kenya	Decock et al. (2021)
	KE-17-228	MT758244	MT758244	–	Kenya	Decock et al. (2021)
H. latisporus	Dai 11873	KU941847	KU941871	MW463008	China	Shen et al. (2016)
H. longisporus	JV 1906/C11-J	MW465685	MW462996	–	Ecuador	Zhou et al. (2021)
H. microsporus	Dai 12147	KU941861	KU941885	–	China	Shen et al. (2016)
H. monomitica	Dai 24229	OP725709	OP725712	–	China	Man et al. (2023)
	Dai 24246	OP725710	OP725713	OP725715	China	Man et al. (2023)
	Dai 24251	OP725711	OP725714	OP725716	China	Man et al. (2023)
H. nanosporus	MUCL 47447	MT782648	MT777438	–	Gabon	Shen et al. (2016)
	MUCL 47559	MT782650	MT777440	–	Gabon	Shen et al. (2016)
H. nepalensis	Dai 12937	KU941855	KU941879	KU941904	China	Shen et al. (2016)
H. odorus	Dai 11296	KU941845	KU941869	KU941894	China	Shen et al. (2016)
	Yuan 2365	KU941846	KU941870	KU941895	China	Shen et al. (2016)
H. papyraceus	Dai 10778	KU941839	KU941863	KU941888	China	Shen et al. (2016)
H. pirongia	Dai 18659	MH631017	MH631021	MW463009	Australia	Zhou et al. (2019)
H. punctatus	Dai19628	MW465687	MW462998	MW463011	Sri Lanka	Zhou et al. (2021)
H. septatus	Cui 4100	KU941844	KU941868	KU941893	China	Shen et al. (2016)
H. srilankensis	Dai19523	MW465688	MW462999	MW463012	Sri Lanka	Zhou et al. (2021)
H. subpapyraceus	Cui 2651	KU941842	KU941866	KU941891	China	Shen et al. (2016)
	Dai 9324	KU941841	KU941865	KU941890	China	Shen et al. (2016)
H. subtrameteus	KUC20121102-36	KJ668536	KJ668389	–	Korea	Shen et al. (2016)
Haploporus sp. 1	LR11231	MT758249	MT758249	–	Malawi	Decock et al. (2021)
H. thindii	Cui 9373	KU941851	KU941875	KU941900	China	Shen et al. (2016)
	Cui 9682	KU941852	KU941876	KU941901	China	Shen et al. (2016)
H. tuberculosus	15559	KU941857	KU941881	KU941906	Sweden	Shen et al. (2016)
Perenniporia citrinoalba	Dai 13643	NR_171808	NG_075212	KX880705	China	Cui et al. (2019)
P. hainaniana	Cui 6364	JQ861743	JQ861759	KF051044	China	Zhao and Cui (2013)

Note: The sequences generated in this study are in bold. "–" represents sequences unavailable.

Zhao et al. 2022b). Four time points were selected for calibration and the offset age with a gamma distributed prior (scale = 20, shape = 1): 1) *Archaeomarasmius leggettii* Hibbett et al. (1995, 1997) represented the divergence time of Agaricales at 90 Mya; 2) *Quatsinoporites cranhamii* S.Y. Sm. et al. (Smith et al. 2004; Berbee and Taylor 2010) represented the Hymenochaetaceae at 125 Mya; 3) *Paleopyrenomycites devonicus* Taylor et al. (Taylor et al. 1999, 2005) represented between Ascomycota and Basidiomycota at 400 Mya; and 4) the estimated mean crown age of Polyporales at 123.74 Mya (Ji et al. 2022). A total of 10,000,000 generations were set, first 20% being burn-in. The results of the log file and trees file were assessed using Tracer v.1.5 and TreeAnnotator v.2.6.5, respectively.

Results

Phylogeny

In this study, dataset 1, including a total of 41 sequences, was used to reconstruct the phylogenetic relationships of the genus *Haploporus* (Table 1, Fig. 1 and Suppl. material 1: file S1). The aligned dataset 1 has a length of 2,797 characters (ITS, 1–783 characters; LSU, 784–2063 characters; and mtSSU, 2064–2797 characters), of which 1,890 are constant characters, 266 are parsimony-uninformative characters and 641 are parsimony-informative characters. The Maximum Parsimony (MP) analysis yielded a tree of length 779, consistency index 0.4856, homoplasy index 0.5144, retention index 0.7658 and rescaled consistency index of 0.3719. The best model for the aligned dataset 1 was GTR + I + G in the Bayesian analysis and the average standard deviation of split frequencies was 0.004282. The phylograms of three analyses, ML, BI and MP, are similar in topology and the ML tree was selected to represent the phylogenetic relationships (Fig. 1).

The phylogenetic analyses indicated that *H. crystallinus* is clustered with *H. nanosporus* and *H. microsporus* and *H. dextrinoideus* formed an independent lineage in the *Haploporus* clade, closely related with *H. grandisporus*, *H. ecuadorensis*, *H. eichelbaumii* and *H. longisporus* (Fig. 1). BLAST results of ITS sequences with the top hit taxa were followed by phylogenetics analyses (Suppl. material 1: table S2).

Divergence times of the *Haploporus*

In the present study, the molecular clock analysis suggested that the order Polyporales and genus *Haploporus* emerged at a mean stem of 159.8 Mya [95% higher posterior density (HPD) of 142.4–184.1 Mya] and 108.3 Mya (95% HPD of 88.5–128.2 Mya), respectively (Fig. 2). A total of 27 species of the genus *Haploporus* was estimated as molecular sequences in *H. brasiliensis* and *H. pileatus* were not available (Lira et al. 2018). The results suggested that species of the genus *Haploporus* may be diversified between 60.5 Mya and 1.8 Mya, during the Paleogene to Neogene in Cenozoic (Fig. 2 and Table 2). Amongst those species, 18 species occurred in the Neogene, accounting for 67% and only nine species originated in the Paleogene.

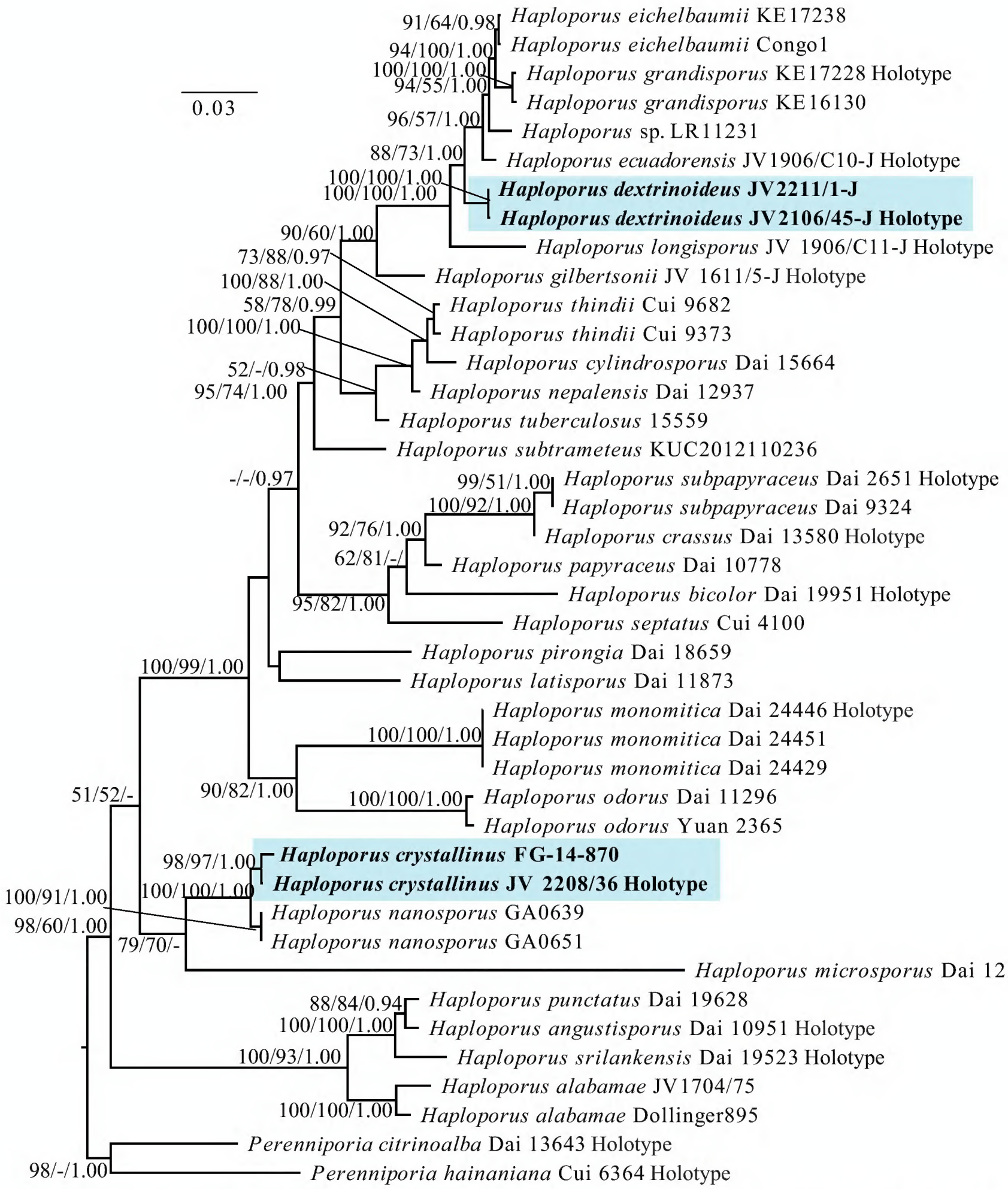


Figure 1. A Maximum Likelihood phylogenetic tree of *Haploporus* based on ITS, LSU and mtSSU gene fragments, with two specimens *Perenniporia citrinoalba* and *P. hainaniana* used as outgroups. The new species *Haploporus crystallinus* and *H. dextrinoideus* are shaded. Maximum Likelihood bootstrap values (≥ 50%)/Maximum Parsimony bootstrap values (≥ 50%)/Bayesian Posterior Probabilities (≥ 0.90) of each clade are indicated along branches. The scale bar left upper indicates the number of substitutions per site.

Taxonomy

***Haploporus crystallinus* H. Zhao, Vlasák & Yuan Yuan, sp. nov.**

MycoBank No: 849261

Figs 3, 4

Etymology. *crystallinus* (Lat.): Refers to the species having many crystals amongst the subiculum and tube trama.

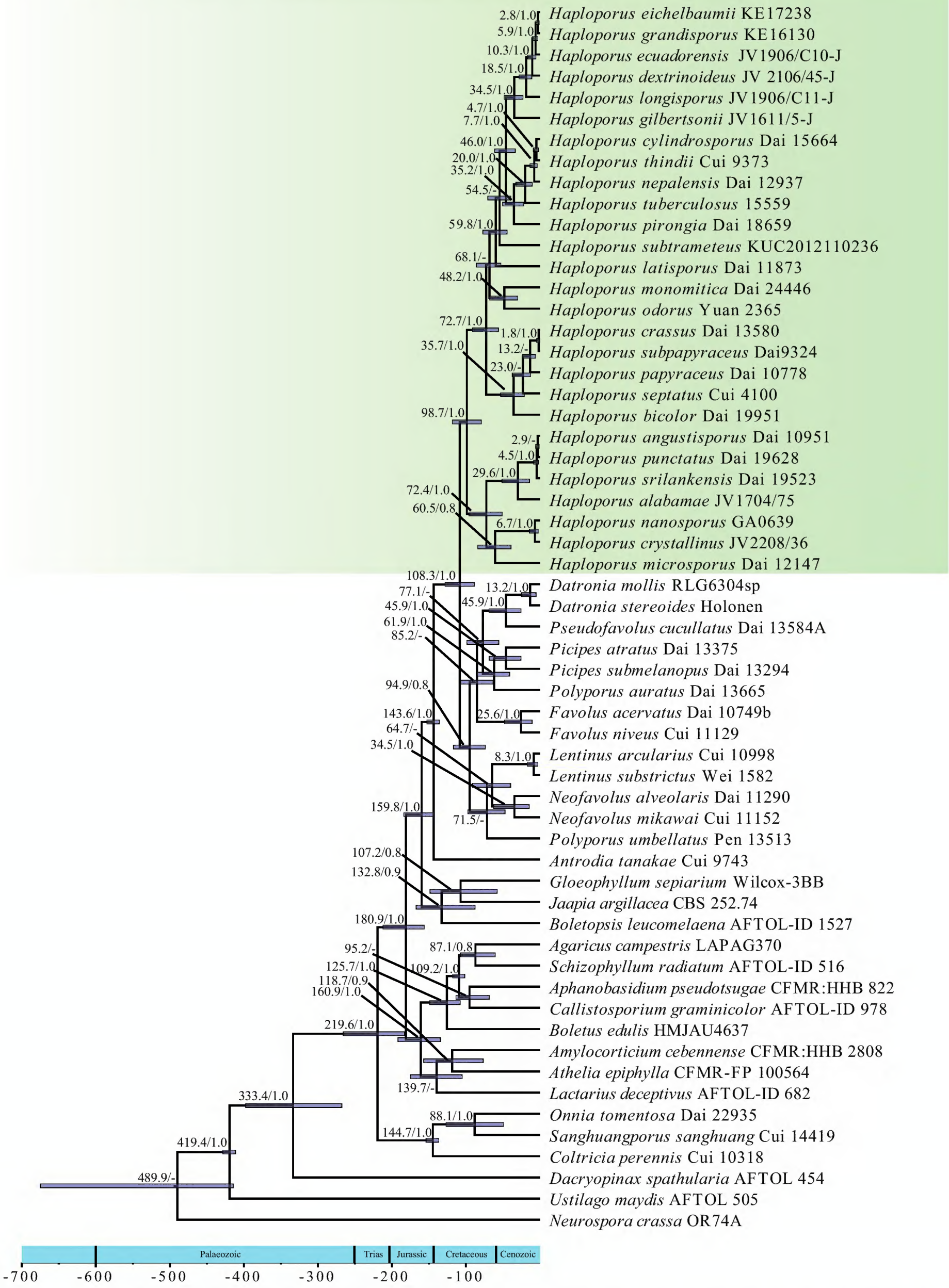


Figure 2. Estimated divergence of *Haploporus* generated by molecular clock analyses using the aligned dataset 2 of ITS and LSU sequences. Estimated mean divergence time (Mya) and Posterior Probabilities (PP) > 0.8 are annotated at the internodes. The 95% Highest Posterior Density (HPD) interval of divergence time estimates are marked by horizontal blue bars. The geological timescale is indicated at the bottom.

Table 2. Divergence times of estimated taxa in the genus *Haploporus*.

Species	Mean of stem in MCC tree (Mya)	95% HPD
Haploporus alabamae	29.6	14.1–51.2
H. angustisporus	2.9	1.1–5.9
H. bicolor	35.7	21.1–53.0
H. crassus	1.8	0.3–4.5
H. crystallinus	6.7	2.3–14.1
H. cylindrosporus	4.7	1.9–8.8
H. dextrinoideus	10.3	5.4–16.8
H. ecuadorensis	5.9	2.7–10.2
H. eichelbaumii	2.8	0.9–5.6
H. gilbertsonii	34.5	23.0–48.3
H. grandisporus	2.8	0.9–5.6
H. latisporus	59.8	52.7–86.0
H. longisporus	18.5	10.9–28.2
H. microsporus	60.5	39.1–84.1
H. monomitica	48.2	23.0–67.8
H. nanosporus	6.7	2.3–14.1
H. nepalensis	7.7	3.6–13.4
H. odorus	48.2	23.0–67.8
H. papyraceus	13.2	6.0–23.8
H. pirongia	35.2	22.1–50.5
H. punctatus	2.9	1.1–5.9
H. septatus	23.0	12.7–37.5
H. srilankensis	4.5	1.9–8.5
H. subpapyraceus	1.8	0.3–4.5
H. subtrameteus	54.5	44.4–77.1
H. thindii	4.7	1.9–8.8
H. tuberculosus	20.0	10.4–32.4

MCC represented as maximum clade credibility.

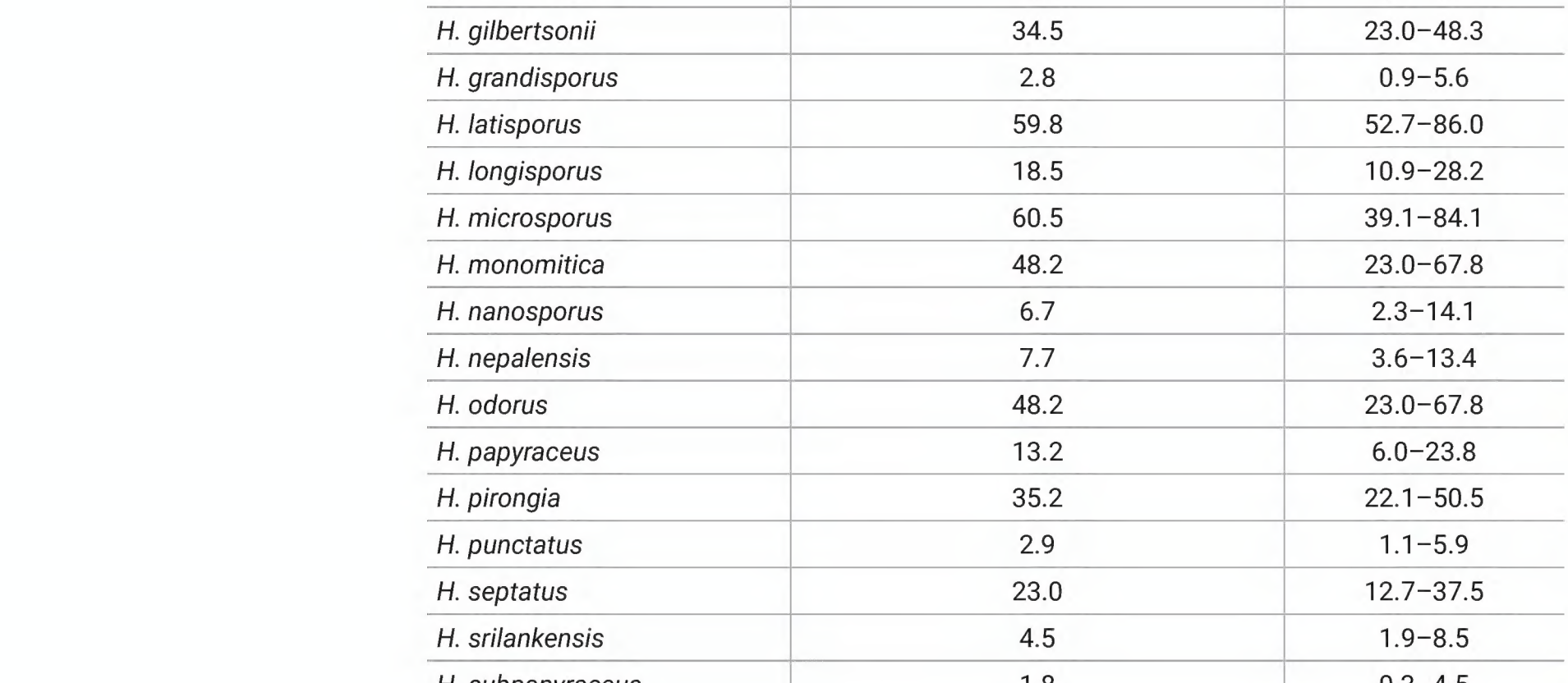
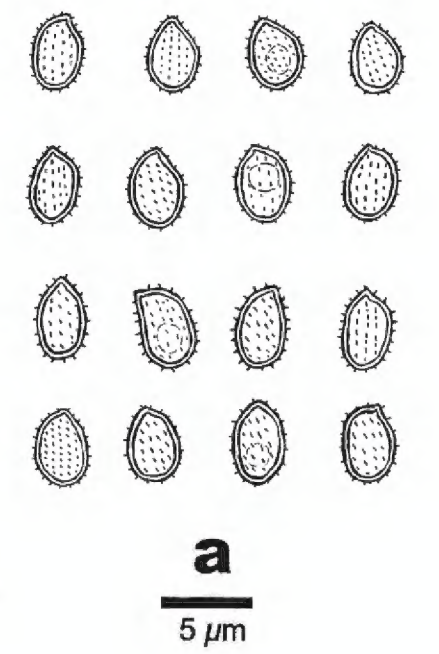
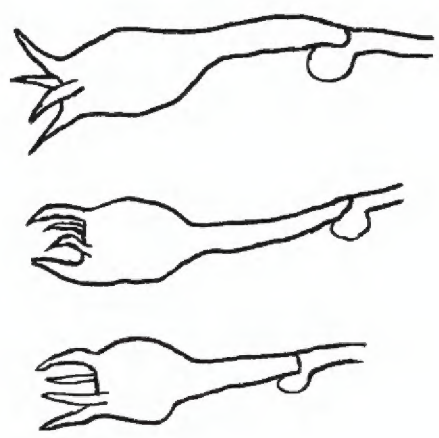
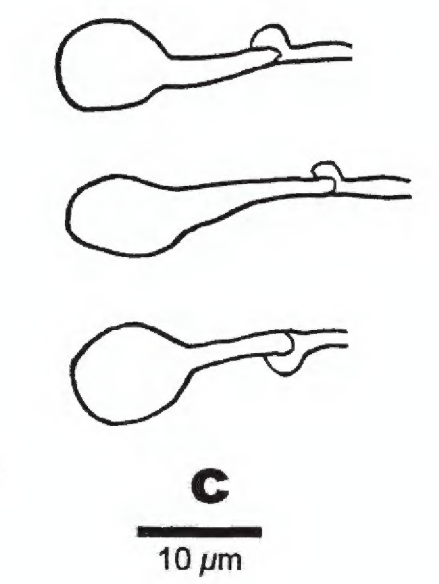
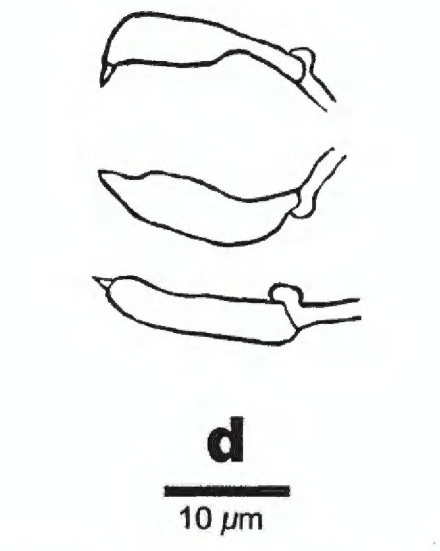


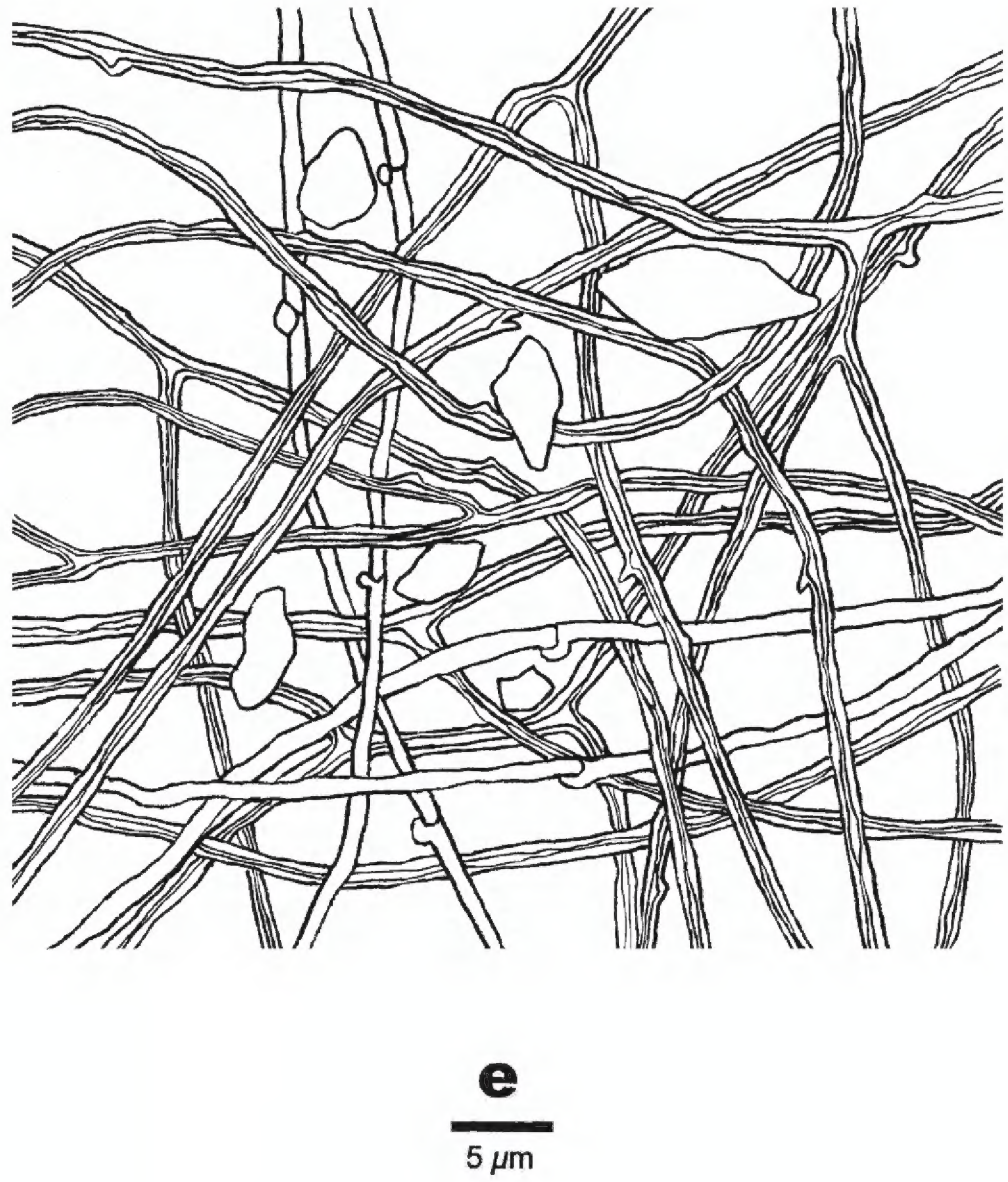
Figure 3. Basidiomata of *Haploporus crystallinus* (Holotype, JV 2208/36). Scale bar: 1 cm.











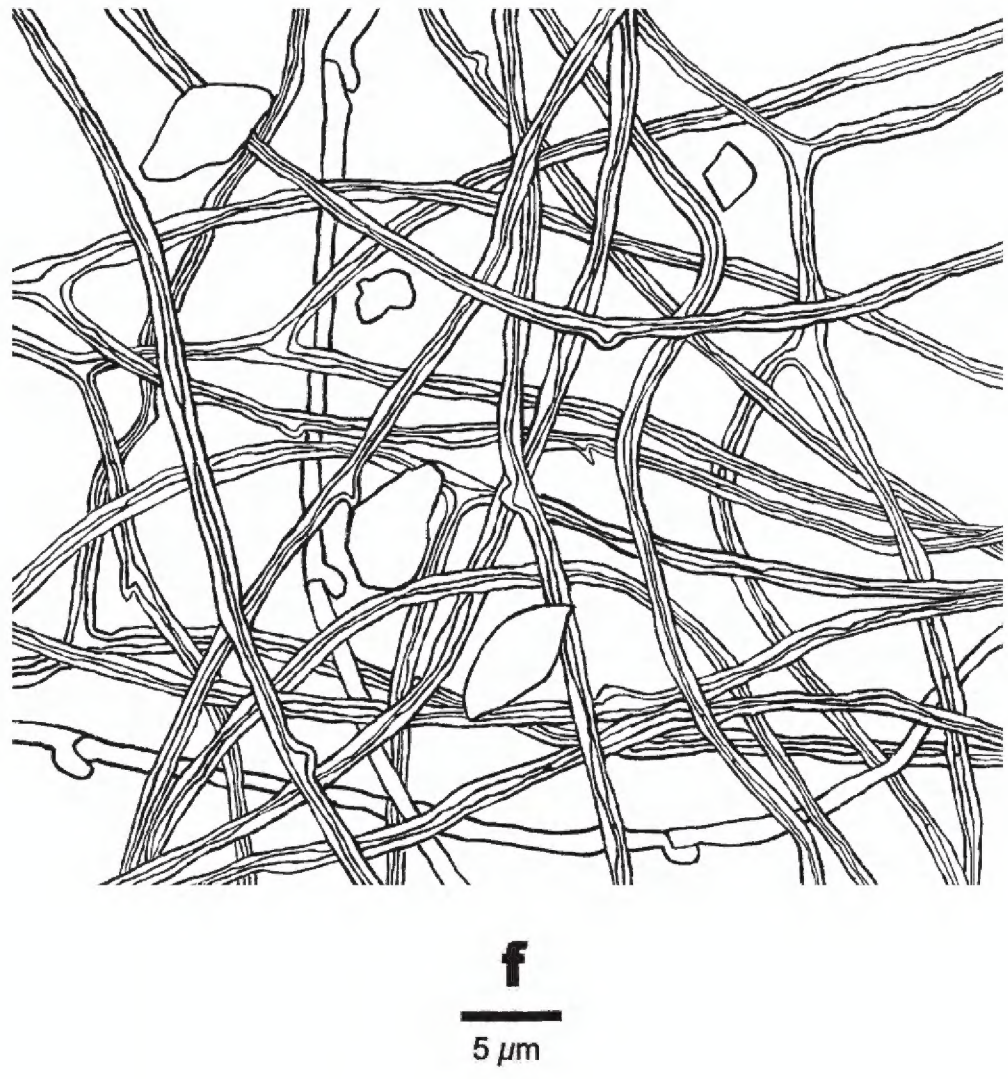


Figure 4. Microscopic characteristics of *Haploporus crystallinus* (Holotype, JV 2208/36) **a** basidiospores **b** basidia **c** basidioles **d** cystidioles **e** hyphae from tube trama **f** hyphae from subiculum. Scale bars: 5 μm (**a**); 10 μm (**b–f**).

Type. French Guiana, Roura, Camp Cayman, rotten log on the road, 27 August 2022, JV 2208/36 (Holotype PRM, isotypes BJFC 039927 and JV 2208/36). GenBank: ITS = OQ919235, LSU = OQ919238, mtSSU = OQ919241.

Basidiomata resupinate, perennial, inseparable from the substrate, more or less corky when dry, up to 10 cm long, 3.5 cm wide and 4 mm thick at centre. Hymenophore pinkish-buff (5A3) to cream buff (4A4) when dry, with indistinct margin; pores angular to round, 5–7 per mm; dissepiments thick, entire. Subiculum darker than tubes, more or less corky. Tubes pinkish-buff (5A3), hard corky.

Hyphal system dimitic; generative hyphae with clamp connections, hyaline, thin-walled; skeletal hyphae thick-walled, frequently branched, distinctly dextrinoid in Melzer's reagent, cyanophilous in Cotton Blue; tissues unchanged in 2% potassium hydroxide.

Subicular generative hyphae infrequent, hyaline, thin-walled, sometimes branched, 1.0–1.5 µm in diam.; skeletal hyphae dominant, with a narrow lumen to subsolid, usually branched, flexuous, interwoven, 0.8–2.0 µm in diam. Irregular-shaped and -sized crystals frequently present.

Tube tramal generative hyphae infrequent, hyaline, thin-walled, sometime branched, 1.0–1.5 µm in diam.; skeletal hyphae dominant, with a narrow lumen to subsolid, usually branched, flexuous, interwoven, 0.8–2.0 µm in diam. Cystidioles fusiform with a sharp tip, thin-walled, hyaline, 12.0–21.0 × 3.0–4.5 µm. Basidia more or less capitate to pyriform, with four sterigmata and a clamp connection at base, 17.5–27.0 × 6.5–9.0 µm; basidioles capitate to pyriform, almost the same size of basidia. Dendrohyphidia absent. Irregular-shaped and -sized crystals frequently present.

Basidiospores ellipsoid, slightly thick-walled, tuberculate, hyaline, some with a guttule, dextrinoid in Melzer's reagent, cyanophilous in Cotton Blue, (3.8–)4.0–5.5 × (2.1–)2.6–3.5(–3.8) µm, L (arithmetic average length) = 4.60 µm, W (arithmetic average width) = 3.03 µm, Q (L/W ratio) = 1.52 (n = 30/1).

Distribution and ecology. *Haploporus crystallinus* is distributed in French Guiana and growing on rotten unidentified angiosperm log; causes a white rot.

***Haploporus dextrinoideus* H. Zhao, Vlasák & Yuan Yuan, sp. nov.**

MycoBank No: 849262

Figs 5, 6

Etymology. *dextrinoideus* (Lat.): Refers to the species having dextrinoid hyphae.

Type. Ecuador, Papallacta Termas, 3,300 m standing dead tree, 15 June 2021, Josef Vlasák Jr., JV 2106/45-J (Holotype PRM, isotypes BJFC 038566 and JV). GenBank: ITS = OQ919236, LSU = OQ919239.

Basidiomata resupinate, annual, inseparable from the substrate, more or less corky when dry, up to 5.0 cm long, 3.0 cm wide and 0.4 mm thick at centre. Hymenophore cream bubalinus (4A2/3) to pinkish-buff (5A3) when dry, margin indistinct; pores angular to round, 1–3 per mm; dissepiments thick, entire. Subiculum slightly darker than tubes, more or less corky, up to 0.2 mm thick. Tubes pinkish-buff (5A3), hard corky.

Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae thick-walled, branched, dextrinoid in Melzer's reagent, cyanophilous in Cotton Blue; tissues unchanged in 2% potassium hydroxide.

Figure 5. Basidiomata of *Haploporus dextrinoideus* (Holotype, JV 2206/45-J). Scale bar: 1 cm.

Subicular generative hyphae hyaline, thin-walled, sometimes branched, 1.0–3.0 µm in diam.; skeletal hyphae dominant, with a wide lumen, usually branched, flexuous, interwoven, 1.5–3.0 µm in diam.

Tube tramal generative hyphae hyaline, thin-walled, usually branched, 1.0–2.5 µm in diam.; skeletal hyphae dominant, with a wide lumen, usually branched, flexuous, distinctly interwoven, 1.0–3.0 µm in diam. Cystidioles fusiform with a sharp tip, thin-walled, hyaline, 19.0–35.0 × 4.5–6.5 µm. Basidia more or less capitate to pyriform, with four sterigmata and a clamp connection at base, sometimes with a few small guttules, 21.0–34.0 × 7.0–14.0 µm; basidioles capitate to pyriform, almost the same size of basidia. Dissepimental hyphae thick-walled with one or four simple septa. Dendrohyphidia present amongst hymenium, thin-walled, hyaline. Large and irregularly-shaped crystals sometimes present amongst trama.

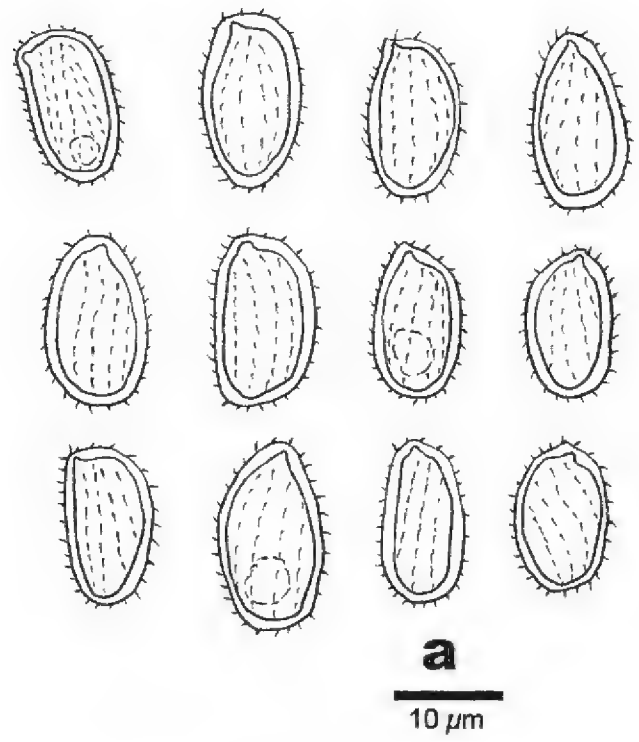
Basidiospores oblong to ellipsoid, thick-walled, tuberculate, hyaline, some with a guttule, dextrinoid in Melzer's reagent, cyanophilous in Cotton Blue, (12.0–)13.2–19.0 × (5.0–)6.0–9.0 µm, L = 15.43 µm, W = 7.78 µm, Q = 1.98–2.16 (n = 60/2).

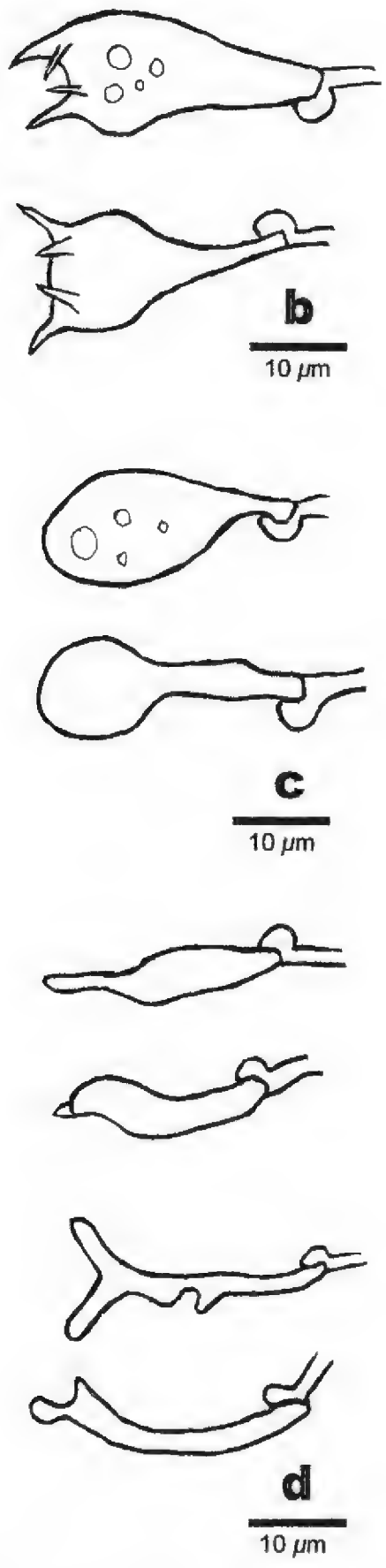
Additional material studied. Ecuador, Papallacta Termas, 3,300 m, on unidentified angiosperm, November 2022, Josef Vlasák Jr., JV 2211/1-J.

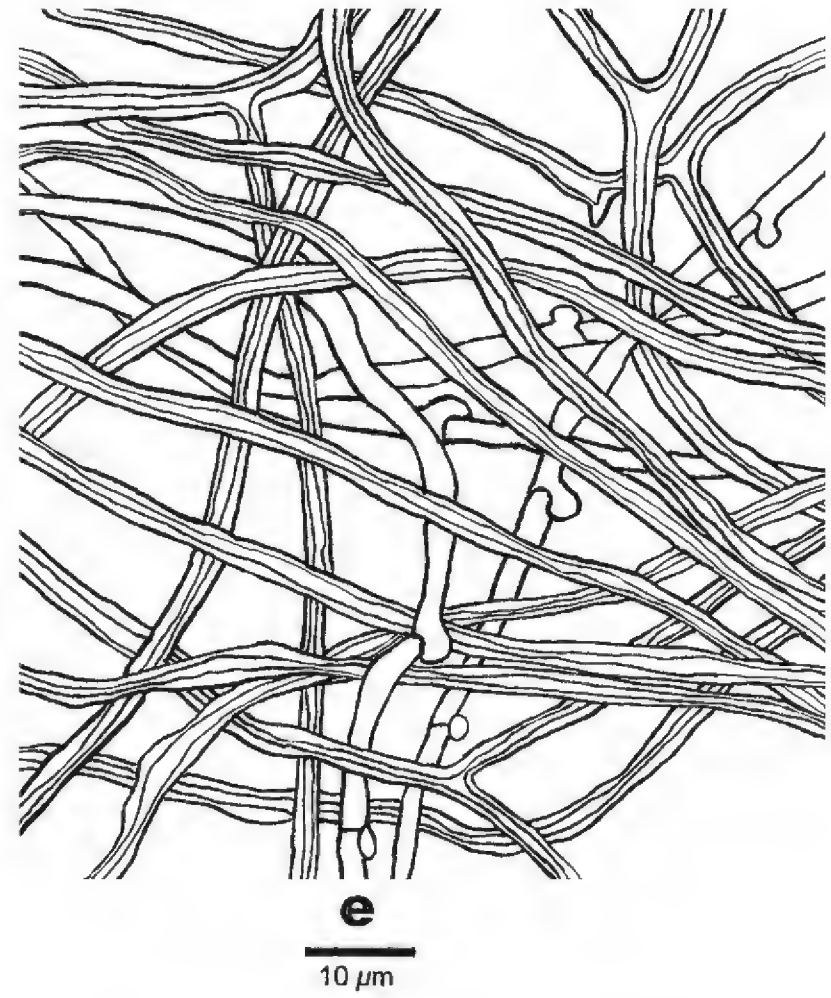
Distribution and ecology. *Haploporus dextrinoideus* is known from Ecuador high mountains, 3,300 m and growing on dead unidentified angiosperm trees; causes a white rot.

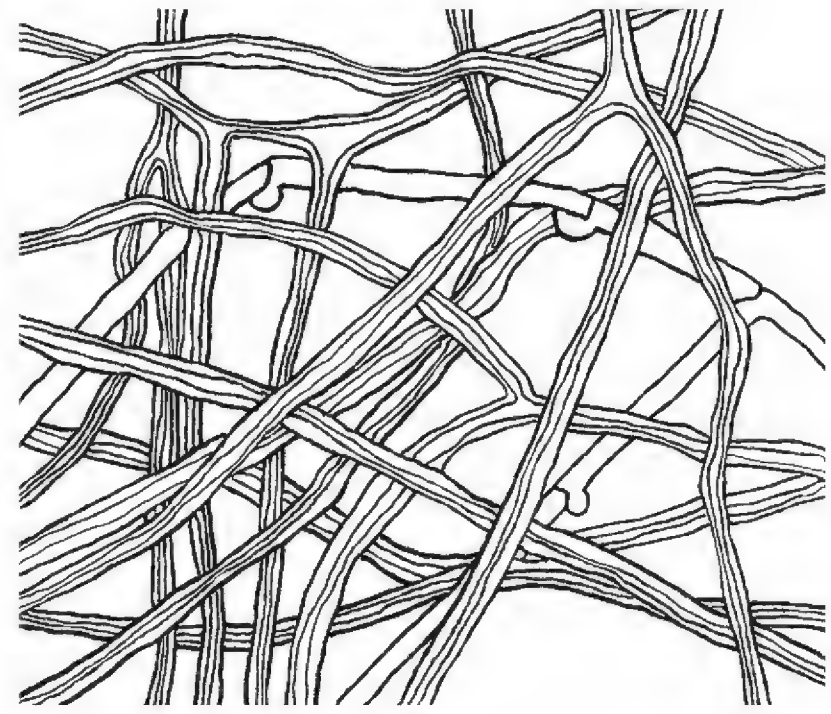
Discussion

Phylogenetic analyses, based on a combined dataset 1 (ITS + LSU + mtSSU sequences), indicates that *H. crystallinus* forms a sister group to *H. nanosporus*









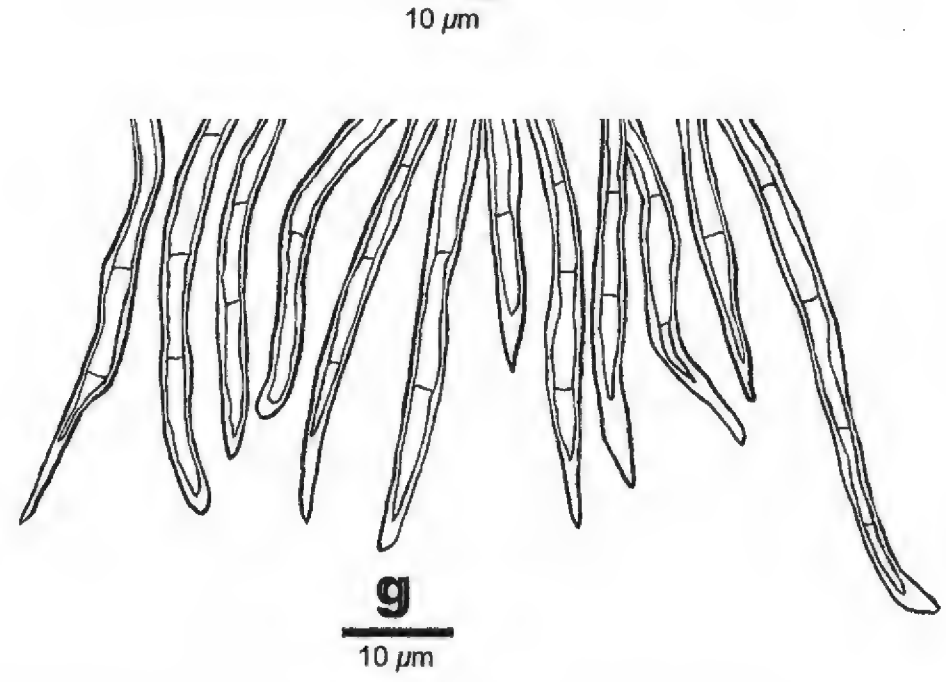


Figure 6. Microscopic characteristics of *Haploporus dextrinoideus* (Paratype, JV 2211/1-J) **a** basidiospores **b** basidia **c** basidioles and cystidioles **d** dendrohyphidia **e** hyphae from tube trama **f** hyphae from subiculum **g** dissepiment hyphae. Scale bars: 10 μm (**a–g**).

and *H. microsporus* with strong support. *H. nanosporus* differs from *H. crystallinus* by rarely branched skeletal hyphae, wider generative hyphae (1.5–2.0 µm vs. 1.0–1.5 µm) and indextrinoid basidiospores (David and Rajchenberg 1992). Additionally, *H. nanosporus* is distributed in Africa (David and Rajchenberg 1992; Decock et al. 2021), while *H. crystallinus* is found in French Guiana, South America. *Haploporus microsporus* differs from *H. crystallinus* by smaller pores (7–9 vs. 5–7 per mm) and annual basidiomata (Zhou et al. 2019). Specimen *Haploporus* sp. FG-14-870 (GenBank numbers: MT782653 and MT777443), collected by Cony Decock on 7 April 2014 in French Guiana, shows ITS sequence similarity with *H. crystallinus* JV 2208/36 over 99%, forming together a clade in the phylogenetic tree. Therefore, *Haploporus* sp. FG-14-870 is another specimen of *Haploporus crystallinus*.

Phylogenetic analyses also suggest that *H. dextrinoideus* forms a clade with the *H. eichelbaumii*, *H. grandisporus*, *H. ecuadorensis* and *H. longisporus* (Fig. 1). *Haploporus eichelbaumii* differs from *H. dextrinoideus* by smaller and indextrinoid basidiospores [11.0–14.0 × 5.3–6.5 µm vs. 13.2–19.0 × 6.0–9.0 µm; Decock et al. (2021)]. *Haploporus grandisporus* differs from *H. dextrinoideus* by narrower skeletal hyphae (1.3–1.8 µm vs. 1.5–3.0 µm), smaller basidia and basidioles (18.0–20.0 × 8.0–13.0 µm vs. 21.0–34.0 × 7.0–14.0 µm) and indextrinoid basidiospores (Decock et al. 2021). *Haploporus ecuadorensis* differs from *H. dextrinoideus* by wider basidioles and basidia (40.0–45.0 µm vs. 19.0–35.0 µm) and hyphae and basidiospores neither amyloid nor dextrinoid (Man et al. 2023). *Haploporus longisporus* differs from *H. dextrinoideus* by the indextrinoid skeletal hyphae and basidiospores (Zhou et al. 2021).

In addition, two species, *H. brasiliensis* and *H. pileatus*, were described in Brazil from South America without molecular data (Lira et al. 2018). *Haploporus brasiliensis* differs from *H. crystallinus* by annual basidiomata, larger pores (1–3 per mm vs. 5–7 per mm), thin dissepiments, wider subicular generative hyphae (2.0–2.5 µm vs. 1.0–1.5 µm) and larger, long-ellipsoid basidiospores [6.0–8.0 × 4.0–5.0 µm vs. 4.0–5.5 × 2.6–3.5 µm; Lira et al. (2018)]. *Haploporus pileatus* differs from *H. crystallinus* by pileate basidiomata, larger pores (3–4 per mm vs. 5–7 per mm), thin dissepiments, cylindrical and larger basidiospores [9.0–10.0 × 4.0–5.0 µm vs. 4.0–5.5 × 2.6–3.5 µm; Lira et al. (2018)]. *Haploporus brasiliensis* differs from *H. dextrinoideus* by smaller basidiospores (6.0–8.0 × 4.0–5.0 µm vs. 13.2–19.0 × 6.0–9.0 µm) and basidia [12.0–15.0 × 4.0–6.0 µm vs. 21.0–34.0 × 7.0–14.0 µm; Lira et al. (2018)]. *Haploporus pileatus* differs from *H. dextrinoideus* by smaller pores (3–4 per mm vs. 1–3 per mm), smaller basidiospores (9.0–10.0 × 4.0–5.0 µm vs. 13.2–19.0 × 6.0–9.0 µm) and basidia [14.0–24.0 × 5.0–7.0 µm vs. 21.0–34.0 × 7.0–14.0 µm; Lira et al. (2018)].

He et al. (2019) estimated the order Polyporales originated at a mean stem of 138 Mya and Ji et al. (2022) suggested that Polyporales originated in the Early Cretaceous, with a mean stem of 141.81 Mya (95% HPD of 102.35–191.91 Mya). Our molecular clock analysis showed that Polyporales originated in a mean stem of 159.8 Mya (95% HPD of 142.4–184.1 Mya), which overlapped previous studies (He et al. 2019; Ji et al. 2022). The genus *Haploporus* emerged at a mean stem of 108.3 Mya (95% HPD of 88.5–128.2 Mya), earlier than the genus *Polyporus* and its allied genera (Zhou et al. 2016; Ji et al. 2022). Species of the genus *Haploporus* probably diversified between 60.5 Mya and 1.8 Mya and 18 species occurred in the Neogene, indicating that species were

rapidly diversified in this period. A similar result is evident in the genus *Onnia*, where most species also appeared in the Neogene (Zhao et al. 2022b).

The study reconstructed the phylogenetic relationships of the genus *Haploporus*, described two new species based on the molecular fragments and morphological evidence. Molecular clock analysis provided insight into the divergence times of *Haploporus* species.

Key to species of *Haploporus*

1 Hyphal system monomitic ..... ***H. monomitica***
1a Hyphal system dimitic to trimitic **2**
2 Basidiospores < 8 µm long **3**
2a Basidiospores > 8 µm long **7**
3 Pores 1–3 per mm ..... ***H. brasiliensis***
3a Pores > 3 per mm **4**
4 Cystidioles absent **5**
4a Cystidioles present **6**
5 Basidiomata annual to perennial, resupinate; pore 7–8 per mm; skeletal hyphae dextrinoid; basidiospores ellipsoid ..... ***H. nanosporus***
5a Basidiomata perennial, effused-reflexed to pileate; pore 3–5 per mm; skeletal hyphae IKI-; basidiospores ovoid ..... ***H. odorus***
6 Basidiomata perennial; pore 5–7 per mm ..... ***H. crystallinus***
6a Basidiomata annual; pore 7–9 per mm ..... ***H. microsporus***
7 Skeletal hyphae dextrinoid **8**
7a Skeletal hyphae non-dextrinoid **9**
8 Basidiomata annual; pore 1–3 per mm; basidiospores 13.2–19.0 × 6.0–9.0 µm ..... ***H. dextrinoideus***
8a Basidiomata perennial; pore 4–5 per mm; basidiospores 8.5–11 × 4–5.2 µm ..... ***H. srilankensis***
9 Basidiospores cylindrical ..... ***H. thindii***
9a Basidiospores oblong ellipsoid to ellipsoid ..... ***H. subtrameteus***
10 Hyphal system trimitic **11**
10a Hyphal system dimitic **13**
11 Skeletal hyphae dextrinoid ..... ***H. tuberculosus***
11a Skeletal hyphae non-dextrinoid **12**
12 Basidiospores ovoid to ellipsoid ..... ***H. alabamae***
12a Basidiospores oblong-ellipsoid to cylindrical ..... ***H. pirongia***
13 Cystidioles absent **14**
13a Cystidioles present **16**
14 Basidiomata pileate ..... ***H. pileatus***
14a Basidiomata resupinate **15**
15 Pores 4–5 per mm, basidiospores cylindrical, 10–11.5 × 4.5–5 µm ..... ***H. cylindrosporus***
15a Pores 1.5–4 per mm, basidiospores ellipsoid to oblong, 10–15 × 5–6.8 µm ..... ***H. eichelbaumii***
16 Dendrohyphidia present **17**
16a Dendrohyphidia absent **21**
17 Pores 5–7 per mm ..... ***H. bicolor***
17a Pores < 4 per mm **18**

18 Basidiospores cylindrical **19**
18a Basidiospores ellipsoid to oblong **20**
19 Basidiospores 18.2–22 × 7–9 µm ..... ***H. longisporus***
19a Basidiospores 13–15 × 5–6 µm ..... ***H. papyraceus***
20 Hyphal system trimitic, skeletal hyphae dextrinoid ..... ***H. grandisporus***
20a Hyphal system dimitic, skeletal hyphae non-dextrinoid ..... ***H. ecuadorensis***
21 Pores > 3 per mm **22**
21a Pores < 3 per mm **26**
22 Pores 5–6 per mm ..... ***H. septatus***
22a Pores 3–5 per mm **23**
23 Skeletal hyphae non-dextrinoid ..... ***H. crassus***
23a Skeletal hyphae dextrinoid **24**
24 Cystidioles without septum ..... ***H. angustisporus***
24a Cystidioles with a simple septum **25**
25 Basidiospores 9–10.8 × 3.8–5 µm ..... ***H. punctatus***
25a Basidiospores 9–12 × 5.5–8 µm ..... ***H. subpapyraceus***
26 Basidiospores 9–10 µm wide ..... ***H. latisporus***
26a Basidiospores < 9 µm wide **27**
27 Basidiospores 12–15 × 6–8 µm ..... ***H. gilbertsonii***
27a Basidiospores 8.5–11.5 × 4.5–6.5 µm ..... ***H. nepalensis***

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

H. Zhao did the drawings, DNA sequencing, data analyses and drafted the paper; J. Vlasák collected and determined specimens and revised the paper; Y. Yuan did the morphological descriptions, revised the paper and provided funding.

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Data availability

The sequences are deposited in the GenBank database (Table 1).

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Supplementary material 1

The supplementary materilas in this study

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Data type: (docx.file, fasta.file)

Explanation note: **figure S1.** A Maximum Likelihood phylogenetic tree of *Haploporus*, based on ITS sequences, with two specimens *Perenniporia citrinoalba* and *P. hainaniana* used as outgroups. The new species *Haploporus crystallinus* and *H. dextrinoideus* are in bold. Maximum Likelihood bootstrap values (≥ 50%) of each clade is indicated along branches. The scale bar left upper indicates the number of substitutions per site. **figure S2.** A Maximum Likelihood phylogenetic tree of *Haploporus*, based on LSU sequences, with two specimens *Perenniporia citrinoalba* and *P. hainaniana* used as outgroups. The new species *Haploporus crystallinus* and *H. dextrinoideus* are in bold. Maximum Likelihood bootstrap values (≥ 50%) of each clade is indicated along branches. The scale bar left upper indicates the number of substitutions per site. **figure S3.** A Maximum Likelihood phylogenetic tree of *Haploporus*, based on mtSSU sequences, with two specimens *Perenniporia citrinoalba* and *P. hainaniana* used as outgroups. The new species *Haploporus crystallinus* and *H. dextrinoideus* are in bold. Maximum Likelihood bootstrap values (≥ 50%) of each clade is indicated along branches. The scale bar left upper indicates the number of substitutions per site. **table S1.** Specimens and GenBank accession numbers used in this study. **table S2.** The top hits of the new species, based on BLAST of ITS sequences from GenBank. **file S1.** All the aligned sequences.

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